ECOGRAPHY

Research

Modelled mid-trophic pelagic prey fields improve understanding of marine predator foraging behaviour

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Ecography
43: 1014–1026, 2020
doi: 10.1111/ecog.04939

Subject Editor: Cagan Sekercioglu
Editor-in-Chief: Miguel Araújo
Accepted 3 March 2020

Biophysical interactions are influential in determining the scale of key ecological processes within marine ecosystems. For oceanic predators, this means foraging behaviour is influenced by processes shaping the distribution of prey. However, oceanic prey is difficult to observe and its abundance and distribution is regionally generalised. We use a spatiotemporally resolved simulation model to describe mid-trophic prey distribution within the Southern Ocean and demonstrate insights that this modelled prey field provides into the foraging behaviour of a widely distributed marine predator, the southern elephant seal.

From a five-year simulation of prey biomass, we computed climatologies of mean prey biomass (average prey conditions) and prey biomass variability (meso-scale variability). We also compiled spatially gridded metrics of seal density and diving behaviour from 13 yr of tracking data. We statistically modelled these metrics as non-linear functions of prey biomass (both mean and variability) and used these to predict seal distribution and behaviour. Our predictions were consistent with observations ($R^2_{adj} = 0.23$), indicating that seals aggregate in regions of high mesoscale activity where eddies concentrate prey. Here, seals dived deeper ($R^2_{marg} = 0.12$, $R^2_{cond} = 0.51$) and spent less time hunting ($R^2_{marg} = 0.05$, $R^2_{cond} = 0.56$), likely targeting deep but profitable prey patches. Seals generally avoided areas of low eddy activity where prey was likely dispersed. Most seals foraged south of the Subantarctic Front, despite north of the front exhibiting consistently high simulated prey biomasses. This likely reflects seal prey or habitat preferences, but also emphasises the importance of mesoscale prey biomass variability relative to regionally high mean biomass. This work demonstrates the value of coupling mechanistic representations of prey biomass with predator observations to provide insight into how biophysical processes combine to shape species distributions. This will be increasingly important for the robust prediction of species' responses to rapid system change.

Keywords: ecosystem modelling, kerguelen plateau, predators prey interaction, micronekton, southern elephant seal, Southern Indian Ocean

Introduction

Understanding how the complex interaction of processes, pattern and scale emerges in real systems remains a fundamental challenge within ecology. Physical and biological processes can affect ecological patterns at a range of scales; from biogeographic influences on community composition and species abundances to fine-scale distribution and behaviour driven by trophic interactions (Levin 1992, Brose et al. 2004, Chave 2013). In pelagic ecosystems, pattern and scale are linked to the underlying oceanography and its spatiotemporal dynamics (Mann and Lazier 2013). Multi-scale oceanographic forcing pervades throughout pelagic food webs and plays a dominant role in shaping the distribution of low to mid-trophic level communities including phytoplankton and zooplankton, as well as the micronekton (i.e. mid-trophic-level, mid-water organisms in the size range of 1–20 cm; Lehodey et al. 2015) that feeds on them. In turn, micronekton represent an important energy link to higher order predators. Thus, understanding the processes that shape micronekton abundance and distribution should underpin knowledge of the foraging behaviour of predators.

However, obtaining synoptic data of micronekton distribution and dynamics is problematic as their biomass is notoriously difficult to observe (Proud et al. 2018). Indeed, despite the significant role micronekton play in mediating energy transfer through the pelagic food web (Saunders et al. 2019), our understanding of their abundance and dynamics remains limited (St John et al. 2016). Sampling of micronekton communities suffers problems of scale, requiring repetition to represent temporal dynamics as well as intensive effort for adequate spatial coverage (Kloser et al. 2009, Escobar-Flores et al. 2018). Observations therefore tend to be patchy in both space and time. Biomass estimates are also confounded by uncertainties around traditional trawl and acoustic sampling methods (Kaartvedt et al. 2012, Proud et al. 2018). To further complicate this, much of the micronekton community undergoes daily vertical migrations from the deep mesopelagic (200–1000 m) during the day to feed in shallower waters (< 200 m) at night (Brierley 2014). Depending on these vertical habits, micronekton groups may be subjected to differential advection by ocean currents (e.g. from the relatively strong and time-varying surface currents to the generally more sedate deep-water flows). This means that their distribution is likely to less directly depend on currents than would be the case for lower trophic-level species (such as zooplankton or phytoplankton) with comparatively reduced swimming capacity.

A mechanistic approach presents the opportunity to overcome some of these limitations and particularly the problem of representing micronekton spatial dynamics. Spatiotemporally resolved physical and biogeochemical models are now becoming sufficiently sophisticated to provide a suitable grounding for simulations that extend beyond primary and secondary producers to micronekton (Lehodey et al. 2010, 2015), as well as pelagic predators (Lehodey et al. 2008, Maury 2010, Senina et al. 2019). In this study, we explore the utility of a mechanistically-derived micronekton field (hereafter referred to synonymously as mid-trophic prey, or prey) for understanding the movements of the southern elephant seal *Mirounga leonina*, a generalist predator that feeds predominantly on mesopelagic fish and cephalopods (Bradshaw et al. 2003, Cherel et al. 2008).

Female seals foraging pelagically tend to use the deep scattering layer (DSL) (McMahon et al. 2019), a biomass-rich micronekton band roughly situated between 300 and 600 m depth (Boersch-Supan et al. 2015). The DSL is heterogeneous, and influenced by dynamic spatial processes that can also act to structure deeper pelagic biomass (Benoit-Bird et al. 2016). We expect that zones of high mesoscale activity (spatial range of 10–100 km, lasting days to weeks) targeted by SES females from Kerguelen Island (Bailleul et al. 2010b, Cotté et al. 2015), where organisms within the DSL are concentrated into dense patches, will be of greater importance to seals than regions of low mesoscale activity where the prey field is less patchy, but still potentially biomass-rich (although see also Massie et al. 2016). To represent mid-trophic prey, we used a new Southern Ocean implementation of the micronekton sub-model of the Spatial Ecosystem And Population Dynamics Model (SEAPODYM; <www.seapodym.eu>), now available from the European COPERNICUS service (<http://marine.copernicus.eu/services-portfolio/access-to-products/?option=com_csw&view=details&product_id=GLOBAL_REANALYSIS_BIO_001_033>). SEAPODYM combines spatially-resolved biophysical variables (including ocean currents, temperature and primary productivity) with allometry, to generate spatiotemporally resolved predictions of pelagic mid-trophic level prey (micronekton) production and biomass. This model has been applied in other regions (at low and mid-latitudes) to successfully represent key forage habitats of predatory fish (Lehodey et al. 2008), turtles (Abecassis et al. 2013), seabirds (Miller et al. 2018) and cetaceans (Lambert et al. 2014).

We show how SEAPODYM can be used to improve our understanding of the distribution and behaviour of southern elephant seals. We do this by 1) using SEAPODYM to represent micronekton distribution at the basin- and mesoscale (patchiness); then 2) developing metrics of seal at-sea distribution and diving behaviour based on 13-yr of satellite tracking data; and 3) modelling these against our simulated micronekton fields to create 4) predictions of important seal foraging habitats. We hypothesise that seals will aggregate and forage more intensely in areas where modelled micronekton are aggregated into dense patches by mesoscale activity.

Methods

Spatial domain

This study focused on the Indian sector of the Southern Ocean (defined here as 45–115°E, 40–65°S) with boundaries

corresponding to the domain of the SEAPODYM implementation. Regional oceanography in this sector is dominated by the eastward flowing Antarctic Circumpolar Current (ACC), its associated fronts (Sokolov and Rintoul 2009), and their interaction with the Kerguelen Plateau. The Kerguelen Plateau is the dominant topographic obstacle to the ACC flow within the sector, forcing its waters and fronts north of 46°S, south of 64°S, or through the deep central Fawn Trough, which splits the plateau into northern and southern parts. The interplay between the ACC and the Kerguelen Plateau leads to distinct flow regimes upstream, over and downstream of the plateau (Bestley et al. 2018, Rintoul 2018). Upstream of the plateau is characterised by zonal flow with little inter-frontal exchange, and low eddy activity in the ACC (Rintoul 2018). Downstream of the plateau, there is complex meandering of the ACC fronts, and the region is eddy-rich with high levels of cross-frontal exchange. Iron fertilization downstream of the northern plateau also allows for the development of an extensive oceanic spring phytoplankton bloom (Van Der Merwe et al. 2015) as well as more persistent productivity around the southern plateau (Schallenberg et al. 2018). The definitions and climatological positions of fronts used here follow Orsi et al. (1995). The Kerguelen Plateau and surrounds is one of the most important regions of primary production within this sector, supporting high-value commercial fisheries of toothfish and icefish over the northern plateau (Duhamel et al. 2011) and large krill stocks farther south (Pauly et al. 2000, Nicol 2006). This region also represents important foraging habitat for large populations of seabirds and marine mammals (Hindell et al. 2011, Raymond et al. 2015, Patterson et al. 2016).

SEAPODYM description

SEAPODYM consists of two sub-models which together simulate the spatio-temporal dynamics of micronekton (mid-trophic prey of 1–20 cm) and the predators that feed on them (Lehodey et al. 2008, Lehodey et al. 2010). Using only the micronekton sub-model of SEAPODYM we simulated mid-trophic prey for the years 2010–2014 at a resolution of 1/12° with a daily timestep. SEAPODYM aims to represent how micronekton redistribute energy originating from surface primary production, through their vertical migratory movements in the water column along with the influence of ocean currents, thus shaping the distribution of energy available for transfer to higher predators (Lehodey et al. 2010). It does this by allocating a portion of total primary production among six functional groups of micronekton that represent the major diel vertical migration (DVM) pathways, and which span three pelagic depth layers (epipelagic, upper mesopelagic and lower mesopelagic) defined by multiples of euphotic depth (Fig. 1). In this way, estimates of micronekton do not represent single target species, but rather multiple mid-trophic species sharing similar vertical habits. The portion of primary production allocated to total micronekton recruitment is determined by an energy transfer coefficient; which is based

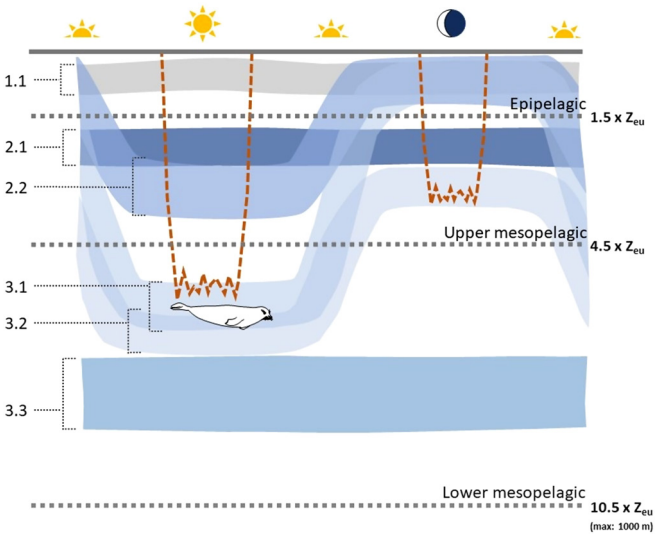

Figure 1. Conceptualisation of the vertical distribution of SEAPODYM functional groups (representing mesopelagic fish, cephalopods and crustaceans within the length range of 1–20 cm) showing vertical migration with time of day. Functional groups represented here as: 1.1 epipelagic, 2.1 non-migrant upper mesopelagic, 2.2 migrant upper mesopelagic, 3.1 highly migrant lower mesopelagic, 3.2 migrant lower mesopelagic, 3.3 non-migrant lower mesopelagic. Depth layers are defined as multiples of Z_{eu} (euphotic depth). Groups shaded in blue were summed for an estimate of available mesopelagic biomass. Superimposed are two typical southern elephant seal dives showing the vertical variation in dive depth. Note that depths of day and night dives span both the upper and lower mesopelagic depth layers.

on the loss of energy across progressive trophic levels. Timing of recruitment and accumulation of biomass over time into these six functional groups are driven by temperature-linked biological time of development, which varies depending on oceanic regions and the amount of time spent within a particular depth layer. Dynamic spatial processes that influence micronekton distribution are implemented as forcing by simulated ocean currents (advection) and random animal movements (diffusion). Forcing variables used in this model are primary production, euphotic depth, depth layer averaged temperature and depth layer averaged horizontal currents. Primary production and euphotic depth are derived from satellite ocean colour data following Behrenfeld and Falkowski (1997). Temperature and currents are calculated by the global eddy-resolving ocean circulation model PSY4v4 of Mercator-Ocean (<www.mercator-ocean.fr/eng>). This model assimilates both satellite (sea surface temperature and height) and in situ data (<http://marine.copernicus.eu/>).

The approach is particularly useful for understanding generalist marine predators, as the functional groups are representative of key prey taxa (mid-water fishes and squids; Bailleul et al. 2010a, Goetsch et al. 2018). An example of daily output can be seen in Fig. 2a, while the model is described in more detail in Supplementary material Appendix 1 S1 and in full by Lehodey (2004) and Lehodey et al. (2010, 2015).

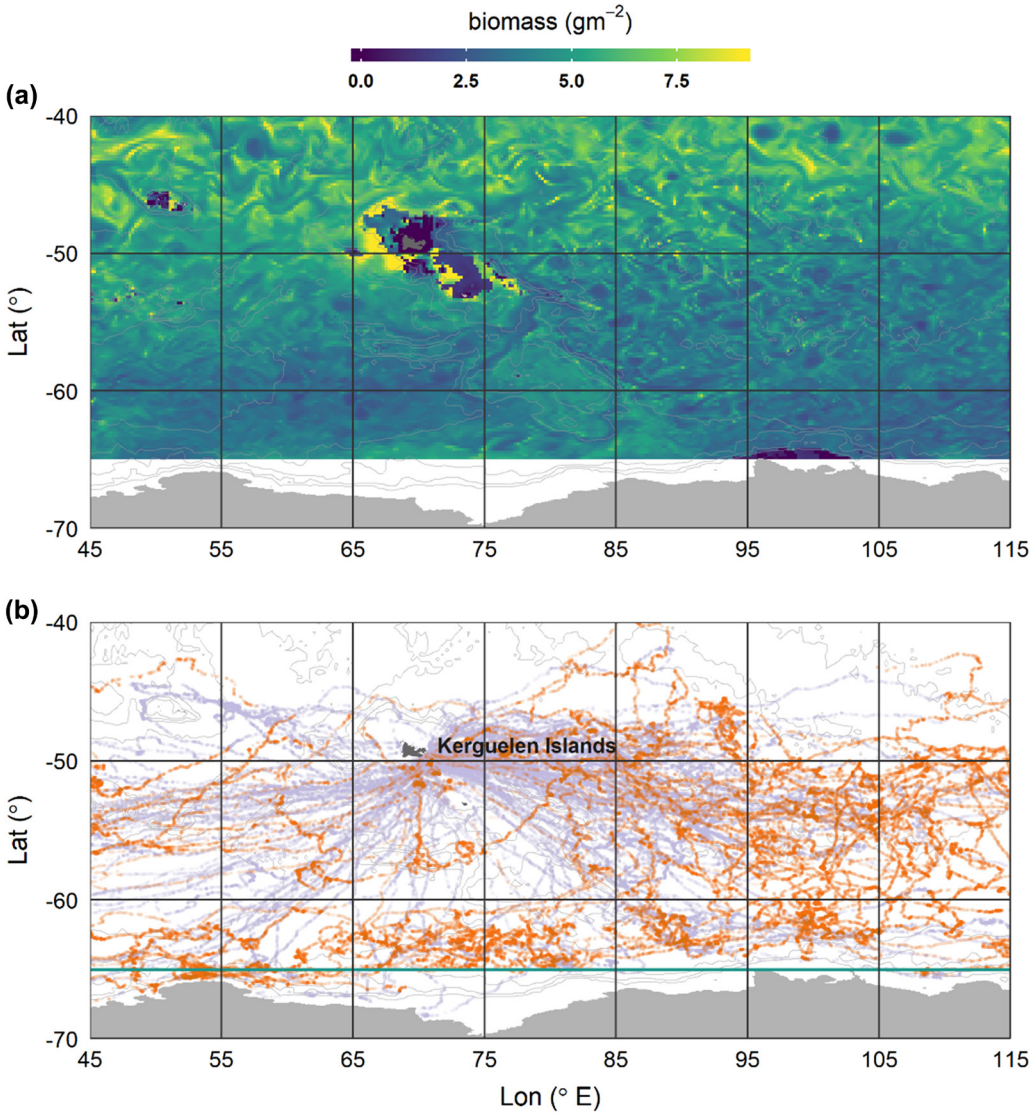

Figure 2. Spatial distribution of (a) modelled prey output and (b) seal tracks for 116 adult female animals during their post-moult migration from February to October. Prey distribution in (a) is an example of the high-resolution model output (1/12°) for non-migrant upper mesopelagic prey biomass on a single day (30 July 2012). (b) shows all tracks across the 13-yr for post-moult adult female southern elephant seals that foraged predominantly in deep water (> 1000 m). Points coloured in orange represent locations recorded during the study period (April–August), whereas light blue points represent locations not included within our analyses (i.e. outside of the April–August window). Green line delineates model extent.

Basin- and meso-scale metrics of prey distribution

Our study domain was the region south of 40 degrees (corresponding roughly to south of the Subtropical Front (STF)), where most elephant seal at-sea activity occurs. Within the Indian sector, female elephant seals dive to depths of, on average, 540 ± 178 m during the day and 402 ± 182 m at night (McMahon et al. 2019), which falls within the upper and lower mesopelagic depth bands (Fig. 1) (Proud et al. 2017, Trebilco et al. 2019). Therefore, we regarded the available prey field as including all those functional groups that are resident in or migrate through the both mesopelagic depth zones (Fig. 1): i.e. both migrant (2.2) and non-migrant upper mesopelagic (2.1) as well as the highly migrant (3.1) and migrant (3.2) and non-migrant (3.3) lower mesopelagic layers. Daily biomass of available prey (hereafter referred to as the available prey field) was then calculated by summing across these groups, and used to build spatial climatologies of prey distribution.

Two metrics were developed to represent the climatological distribution of prey at coarse and moderate (meso) temporal scales. Metric 1 – mean prey biomass: to represent average prey conditions, we calculated mean prey biomass across the full model period, effectively removing the short-term variability in biomass associated with mesoscale activity. Metric 2 – prey biomass variability: to explicitly consider the

role of mesoscale processes in aggregating prey, we calculated monthly variability of the daily output over the five years, thus giving us biomass variability. Mesoscale eddies serve to maximise foraging profits for seals (Dragon et al. 2010, Della Penna et al. 2015, Abrahms et al. 2018) by concentrating DSL biomass through entrainment and local enhancement, giving rise to distinct high-biomass patches particularly at the edges of eddies, with lower biomasses on either side (Sabarros et al. 2009). High levels of prey biomass variability would result from these prey patches being advected, by mesoscale processes such as eddies, through a given location over time. From an Eulerian perspective, this should give rise to high location-based prey biomass variation before, during and after passage of an eddy. The rate of this biomass variability should be roughly one month, equivalent to the average length-scaled displacement time estimated for ACC eddies (Park et al. 2002). It is also important to note that due to the chaotic nature of eddies (Pratt et al. 2014), circulation models are unlikely to forecast their exact location in space and time. However, under conditions averaged over time, modelled and actual fields should provide reasonable spatial representation of areas (grid cells) where high mesoscale activity occurs. Consequently, we chose the mean monthly coefficient of variation (cv) of prey biomass per spatial grid cell across the five simulation years as a climatological representation of dynamic mesoscale prey distribution.

We focused upon the months of April–August to create our climatologies, to align with the foraging trips of seals (see below). During dispersal from the colony adult females may be driven more by intrinsic factors than by the availability of prey; we reduced the effect of these intrinsic factors by considering only the period when seals are most likely to be in their foraging areas. The two prey field climatologies were interpolated on to a $1° \times 1°$ grid to directly relate to our marine predator usage metrics. A coarse grid would reduce resolution, but there is a necessary trade-off between coverage and resolution. We chose this resolution to minimise the number of empty cells, thereby ensuring adequate spatial coverage of our observational dataset.

Elephant seal tracking data

We used adult female southern elephant seals, which predominantly forage pelagically in the open ocean (Campagna et al. 1995, Bailleul et al. 2010a). From 2005 to 2018, 251 adult females were tagged at Kerguelen Island with Conductivity-Temperature-Depth Satellite Relay Data Loggers (CTD-SRDL-9000 – Sea Mammal Research Unit, St Andrews, UK) prior to the onset of their post-moult migration (Roquet et al. 2014, Treasure et al. 2017). Full tagging details have been published elsewhere (Hindell et al. 2016). At-sea seal movements were determined through the ARGOS satellite tracking system (Roquet et al. 2014, Treasure et al. 2017). Due to the irregular timing and errors associated with ARGOS location data, these were filtered using a state-space model to obtain a regular 2 h time step of location estimates with reduced uncertainty (Jonsen et al. 2018).

We only included females that foraged pelagically in deep (> 1000 m) waters as seals that forage over shelf regions (Kerguelen plateau or Antarctic shelf) predominantly perform benthic dives, likely targeting benthic prey rather than micronekton (O'Toole et al. 2014). We focused on oceanic foragers by retaining all individuals with at least 60% of their locations associated with waters deeper than 1000 m, based on estimates of bottom topography (ETOPO1 bathymetry, <www.ngdc.noaa.gov/mgg/global/>). Similarly, to eliminate any benthic diving that may have taken place along the shelf or slope, we excluded all dives with maximum depths within 20 m of the sea floor. Elephant seals are also known to perform various dives in which they do not actively search for prey (Dragon et al. 2012, Arce et al. 2019), so we removed all dives in which the seal recorded less than 60 s hunting time (see below for details). To exclude periods of dispersal during the beginning and end of the post-moult migration, we only considered tracks for which we had locational data from April through August. The final dataset consisted of 66 individual seals and tracks (Fig. 2b).

Metrics of predator distribution and foraging effort

We gridded ($1° \times 1°$ spatial resolution) seal location and dive data into metrics of distribution (seal density) and foraging effort. A satellite relayed data loggers (SRDL) transmits highly summarised dive information, reducing each dive profile to five segments delineated by the six main inflection points of the full profile (Heerah et al. 2015). For each dive, maximum dive depth (m), hunting time (s) and a dive residual (as defined below) were calculated. Hunting time, the duration of time spent in active prey search, was calculated following (Heerah et al. 2015). Hunting time is an index of vertical sinuosity within a dive to determine the duration spent in active foraging, indicated by those segments with a rate of change less than $0.4\ m\ s^{-1}$. This method has been validated against accelerometer-inferred prey capture data, where segments classified as active hunting were associated with 68% of prey capture attempts, and outperformed similar metrics for inferring hunting behaviour (Heerah et al. 2015). As dive depth increases, so too must the duration of descent and ascent. The dive residual – the residual of the dive depth versus dive duration regression (Bestley et al. 2015) – is a practical means of determining whether a dive is relatively long or short for a given depth (although see also Jouma'a et al. 2016).

Comparisons between seal metrics and the modelled prey field were performed over the months April–August. Using our filtered dataset, we calculated a metric of seal distribution, defined as the number of seals visiting each grid cell over the 13 years of available data; and three metrics of foraging effort, defined as the mean maximum depth, hunting time and dive residual per individual per grid cell. The time-window of the simulation falls in the middle five years of the 13-yr tracking dataset and we use climatologies of the two periods to ensure that the two datasets can be analysed together meaningfully. All analyses were conducted using R 3.5.1 (R Core Team).

Modelling predator responses to prey

Prior to fitting statistical models, we assessed the data for the presence of outliers in the simulated prey information, removing values beyond the 1–99% quantile range. This removed a small number of observations from our seal distribution (50; final n = 1171) and effort (95; final n = 2473) datasets. We anticipated a non-linear relationship between seal and prey covariates, so adopted a generalised additive model (GAM) framework (package mgcv; Wood 2011). Seal distribution was modelled against mean prey biomass and prey biomass variability using a simple fixed-effects model (GAM) assuming a negative-binomial error structure and logarithmic link function. The hunting time, dive residual and mean maximum depth models were fitted using the same fixed effects, but with the addition of a random effect for individual seals using a generalised additive mixed model (GAMM), with a gaussian error and identity link function. In all models, we restricted our functional smooths to a maximum of $k = 5$ (the basis dimension for the penalized regression smoothers) to avoid overfitting. The fit of each model was assessed using restricted maximum likelihood (REML) estimation. Our models were specified as follows:

Seal distribution model: $n.seals \sim s(biomass) + s(variability)$
Hunting time model: $hunting.time \sim s(biomass) + s(variability)$, $random = list(seal.id = \sim 1)$
Dive residual model: $dive.residual \sim s(biomass) + s(variability)$, $random = list(seal.id = \sim 1)$
Dive depth model: $dive.depth \sim s(biomass) + s(variability)$, $random = list(seal.id = \sim 1)$

Where *biomass* and *variability* represent mean prey biomass and prey biomass variability respectively.

We used the fitted models to predict seal distribution and foraging behaviour across the full spatial domain, the latter based upon fixed effects only to predict population-level responses. To ensure all predictions were reported in the original units, model estimates of seal number were first back-transformed from the log-scale.

Results

Mid-trophic prey distribution

The mean biomass of prey groups available in the upper and lower mesopelagic was $4.57 \pm 1.08\ g\ m^{-2}$ across the spatial domain (Fig. 3a). Mean prey biomass in oceanic waters was highest north of the Antarctic Polar Front (APF), except for a region of relatively high biomass in the far south between 65°E and 75°E. South of the APF, mean prey biomass remained low and was lowest in the area west of the southern Kerguelen plateau. The northern plateau showed the highest and the lowest mean prey biomasses, west and east of the Kerguelen Islands respectively, whereas the southern plateau consistently supported an intermediate mean prey biomass.

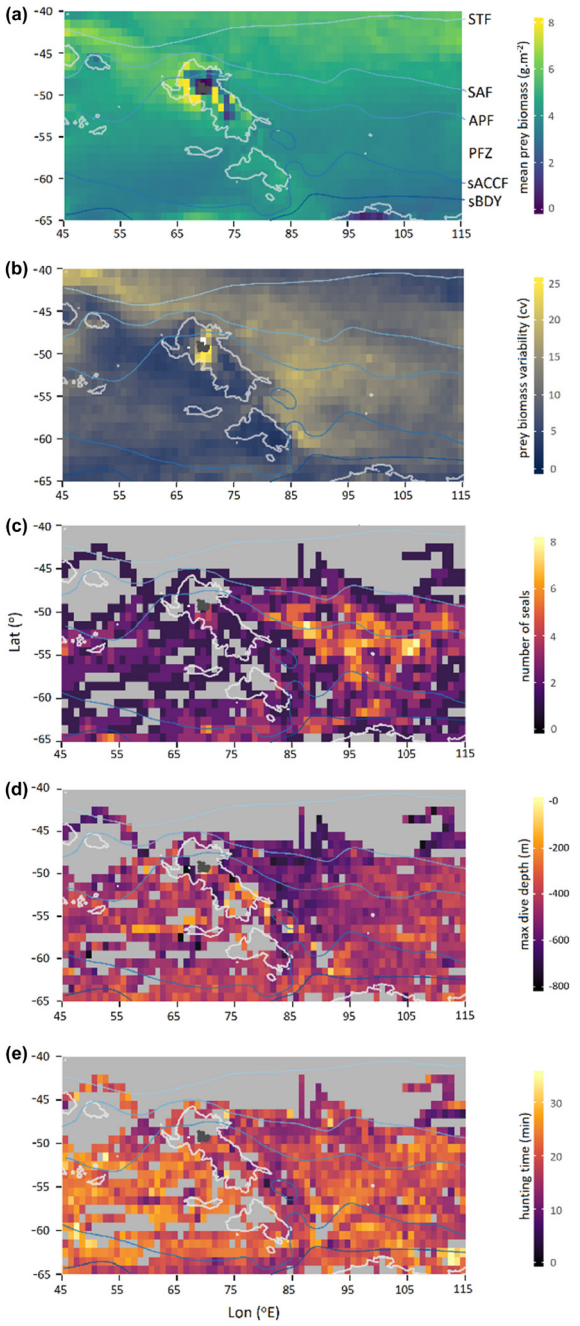

Figure 3. Spatial distribution of prey and elephant seals within the spatial domain at 1° resolution. Broad- and meso-scale distribution of prey is represented by full-span climatologies of (a) mean prey biomass and (b) mean coefficient of variation of functional groups occurring within the upper and lower mesopelagic. Observed number of seals, and mean maximum depth and hunting time per dive are given by (c), (d) and (e) respectively. The Kerguelen plateau and Antarctic shelf are given by the 2000 m isobath, coloured in grey. Major oceanic fronts in order from the north are: STF (Sub-tropical Front), SAF (Subantarctic Front), APF (Antarctic Polar Front), PFZ (Polar Frontal Zone), sACCF (southern Antarctic Circumpolar Current Front) and sBDY (Southern Boundary Front) (Orsi et al. 1995). The location of the Kerguelen archipelago is centred within the northern Kerguelen plateau.

Patterns in prey biomass variability (Fig. 3b) were oriented along a north–west to south–east axis mirroring the dynamic eddy field of the ACC (Park et al. 2009, Rintoul 2018). High prey biomass variability was evident in a narrow band north of the Crozet Islands and the northern Kerguelen plateau, which broadened as it extended southwards downstream of the plateau. Areas of highest variability occurred immediately east of the central and southern plateau, north of the Crozet Islands and over the plateau around the Kerguelen Islands. The margins of these features and the polar frontal region to the far east of the domain had intermediate levels of variability probably caused by dissipating eddy kinetic energy. Prey showed the lowest variability across the southern plateau and in the west of the study domain where eddy kinetic energy is typically low (see Fig. 3 of Mori et al. 2016). In general, areas of elevated prey biomass variability tended to have low biomass, that is, mean prey biomass and prey biomass variability appear as inverses of one another (Fig. 3). A detailed description of the output for the SEAPODYM individual functional groups can be found in Supplementary material Appendix 1 S2.

Seal distribution and foraging effort

During April–August (austral autumn/winter) female elephant seals foraging pelagically visited 63% (n = 1140) of the 1° × 1° cells within the spatial domain (Fig. 3c). Seal numbers per cell ranged up to eight with a median of two. Most individuals dispersed to the east of the plateau with highest numbers in the polar frontal zone (PFZ). Another area of high visitation was between 60°E and 90°E south of 63°S. Few seals were recorded north of the SAF and likewise individuals mainly traversed through the area west of the Kerguelen plateau.

A correlation matrix indicated significant correlation between dive residuals and dive depth as well as hunting time, but not between the latter two variables (Supplementary material Appendix 1 S3). As such, we report here the results for dive depth and hunting time (Fig. 3d–e) and include the dive residual output in Supplementary material Appendix 1 S3. Mean dive depth, per seal per grid cell, was 473 ± 112 m and hunting time was 20 ± 4.8 min. While not correlated, seal behaviour tended to show broadly inverse spatial patterns between dive depth and hunting time. On average, seals in areas of high eddy activity northwest and immediately east of the northern plateau performed relatively deep dives where they spent comparatively little time actively hunting. Across seals, mean dive depth was generally shallowest and hunting time greatest in the PFZ; particularly in the far west of the domain near 45°E (452 ± 100 m, 23 ± 3.8 min) as well as in the PFZ broadly east of 90° (451 ± 71 m, 20 ± 3.8 min). The southern Kerguelen plateau was also associated with relatively shallow dive depths (448 ± 112 m) and high mean hunting times (19 ± 2.8 min).

Model fit

In our seal distribution model, mean prey biomass and prey biomass variability together explained 26% ($R^2_{adj} = 0.23$) of the variation (model deviance) in the number of seals per grid cell. Seal numbers increased slightly up to a mean prey biomass of 4 g m^{-2} before decreasing (Fig. 4a). In contrast, seal numbers increased linearly with increasing prey biomass variability. These two predictors when considered alone explained less of the overall variation in our models for hunting time ($R^2_{marg} = 0.05$) and dive depth ($R^2_{marg} = 0.12$), but the inclusion of individual as a random effect significantly improved model fit ($R^2_{cond} = 0.56$ and $R^2_{cond} = 0.51$ for hunting time and dive depth respectively). Mean maximum depth increased in relation to both increased mean prey biomass and prey biomass variability (Fig. 4b). Overall, hunting time showed broadly inverse trends, decreasing rapidly with increasing mean prey biomass and remaining fairly stable up to intermediate prey biomass variability (cv = 10) but dropping steeply thereafter (Fig. 4c). A full summary of the model fits can be found in Supplementary material Appendix 1 S4 Table A1.

Spatial predictions of seal distribution and foraging effort

Based on our models, predicted seal numbers were highest in the highly dynamic eddy field east of the central and southern Kerguelen plateau, centred around 85°E, and also north–west of the plateau (Fig. 5a). The fewest female seals were predicted to use waters south of the Southern Boundary (sBDY) between 85°E and 105°E and north of the SAF. Likewise, few seals were predicted over the central part of the Kerguelen plateau and in open ocean immediately west of both the northern and southern sections of the plateau. These results support the first half of our hypothesis that seals would aggregate in regions where mesoscale activity aggregated their prey.

Predicted dive behaviour south of the SAF, where most seals foraged, generally mirrored the patterns in seal number. The deep ocean habitat immediately east of the plateau and frequented by seals was predicted to be characterised by deep dives (> 500 m) with relatively short hunting times (< 20 min). Similar patterns were also predicted for the region north–west of the Kerguelen plateau. The converse was true for the region west of the plateau, where seals were predicted to undertake shallower dives (< 500 m) and expend more time in active hunting (> 22 min). Contrary to our hypothesis, these results suggest a decrease in seal foraging effort where seals gather around mesoscale activity that aggregates the mid-trophic prey field. North of the SAF, where few seals ventured, dives were predicted to be deep and characterised by very short hunting times (although these predictions are based on few observations). Shallow dive depths along with short hunting times were also predicted over the southern Kerguelen plateau. Our prediction maps generally conformed well to the observational dataset. On average, predicted values differed from observations by 1 ± 0.8, 74 ± 67 m and 4 ± 2.9 min for seal density, maximum dive depth and hunting time respectively. Differences between predicted and observed seal density and behaviour are displayed along the right-hand column of Fig. 5, while standard errors around

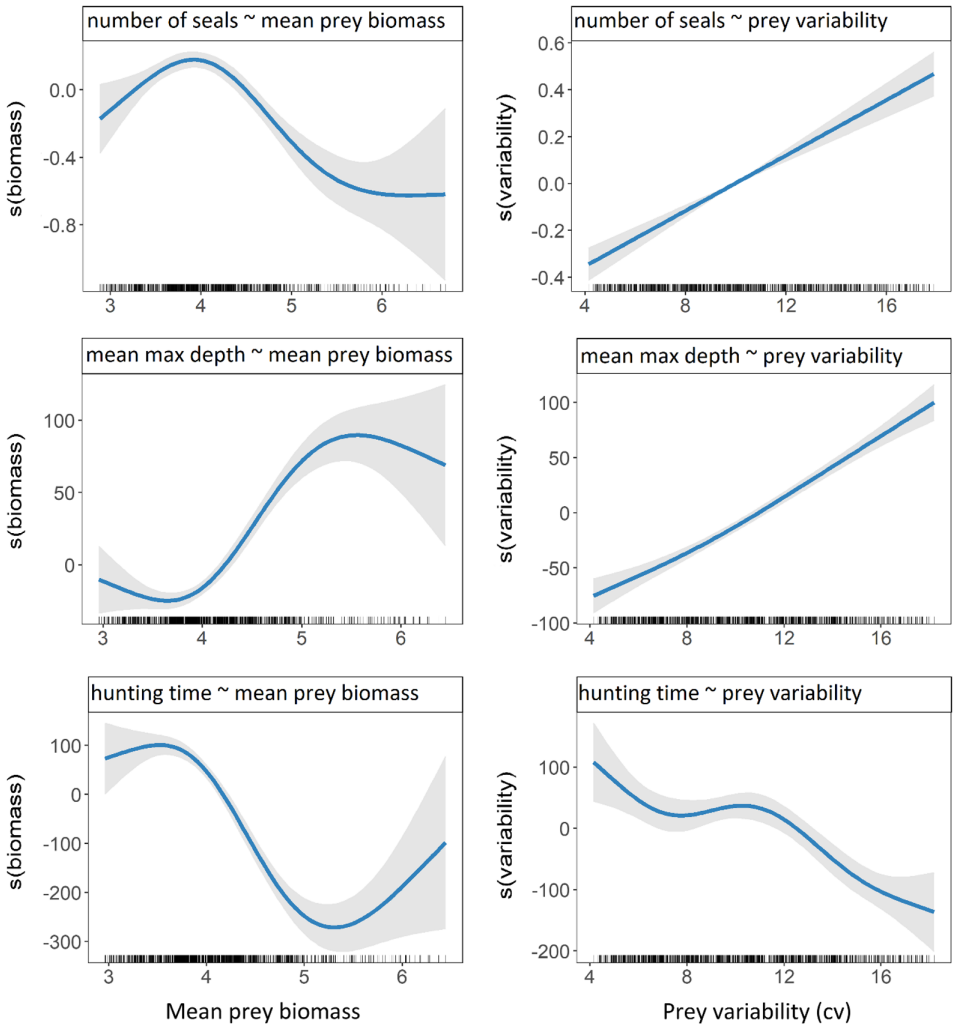

Figure 4. Partial regression plots showing smooths of GA(M)M terms for the effect of prey biomass (mean and variance) on seal distribution (number of seals) and foraging effort (mean maximum depth and mean hunting time). Panel titles indicate Response ~ Predictor variables. Solid blue lines are the estimates of the smooths and shaded areas indicate 95% confidence intervals (two standard error bounds) of the estimated smooths. Locations of observations are shown as vertical lines on the x axes.

these spatial predictions are displayed in Supplementary material Appendix 1 S3.

Discussion

Here, we use modelled prey fields to provide new insights into the distribution and dynamics of mid-trophic pelagic prey (micronekton) and its influence on predator behaviour in the Indian sector of the Southern Ocean. We show that the modelled prey fields provide valuable information, at both coarse- and mesoscales, which can be used to make meaningful biological inferences about the movement and foraging behaviour of a wide-ranging marine predator. We found that female elephant seal density peaked within the dynamic ACC eddy field east of the Kerguelen plateau, where mesoscale activity drives prey biomass variability. Furthermore, regions predicted to support high seal numbers were characterised by deep dives with relatively little active hunting.

Few seals ventured into regions of consistently high prey biomass, but little prey biomass variability; for example, in the north of the study domain, or south of the Southern Boundary of the ACC. This suggests that processes causing mesoscale variability in prey biomass were more important to foraging seals than processes that drive high mean prey biomasses at a broader (regional) scale. The analysis of SEAPODYM output in relation to observational metrics (for distribution and behaviour) obtained from satellite-tagged seals, clearly demonstrated the relevance of including mesoscale prey distributions to help interpret predator foraging behaviour.

Predators tend to have higher success in regions where biophysical features aggregate prey (Robinson et al. 2010, Abrahms et al. 2018, Rivière et al. 2019). High prey densities are particularly useful for deep-diving predators like elephant

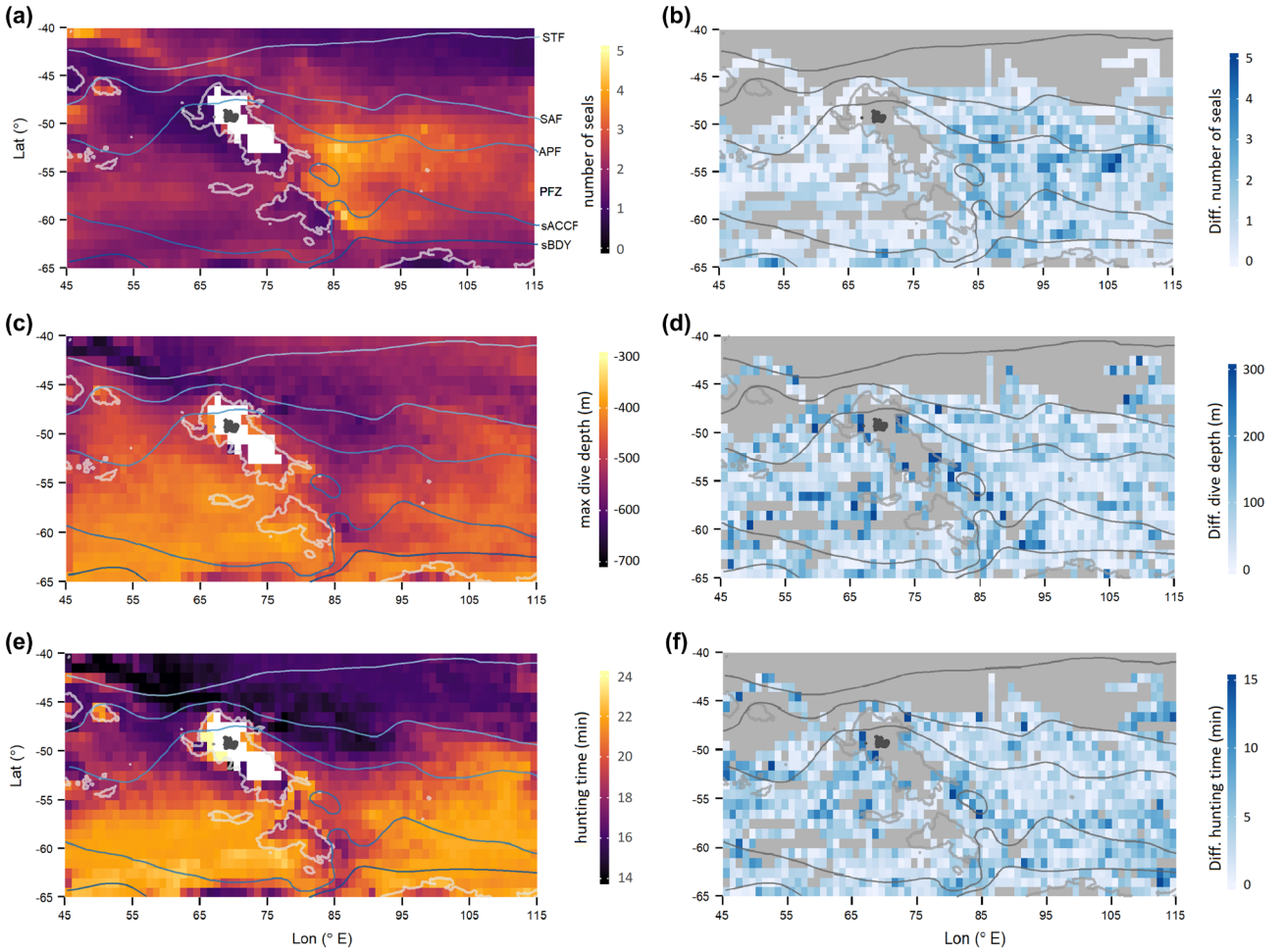

Figure 5. Predicted (a) seal density, (c) mean maximum dive depth and (e) mean hunting time per 1° cell based on functional GA(M)M smooths. Panels (b), (d), (f) on right denote the differences between predicted and observed mean values for each of these three variables. Missing cells in the left-hand column represent mean bathymetry shallower than 1000 m. Frontal features are: STF (Sub-tropical Front), SAF (Subantarctic Front), APF (Antarctic Polar Front), PFZ (Polar Frontal Zone), sACCF (southern Antarctic Circumpolar Current Front) and sBDY (Southern Boundary Front) (following Orsi et al. 1995).

seals that spend much of their time beneath the euphotic zone where limited light probably reduces prey detection range (Naito et al. 2013, although see also Vacquié-Garcia et al. 2012). Our GA(M)M approach indicated an increase in seal numbers in association with increased prey biomass variability (a proxy for patchiness), implying that the most suitable foraging habitats for seals are highly heterogenous and likely to be characterised by dense prey patches. Unlike deep-diving cetaceans that make use of echolocation, elephant seals locate prey passively, which gives them a narrower field of detection. Targeting areas with high densities could be a strategy for overcoming this by maximising prey encounter rates (Naito et al. 2013). This seems to be supported by the low number of seals in waters west of the plateau where the absence of strong mesoscale forcing likely prevents dense prey patch formation.

South of the SAF and within areas of high prey biomass variability and patchiness, where seals were in highest numbers, the GA(M)Ms also indicated that seals dived deeper and spent relatively little time actively hunting, and dive durations were comparatively shorter than expected for the given depths (Supplementary material Appendix 1 S4). Following optimal foraging theory, Thompson and Fedak (2001) and Sparling et al. (2007) proposed that divers should optimise net energy gain by choosing to abort dives early when prey encounter rates are below a certain threshold, but increase bottom time at high rates of encounter. This might suggest that seals congregating east of the plateau are foraging in low quality habitat. However recent work on free-ranging elephant seals has shown that dive duration and bottom time do not increase with increased patch quality (Thums et al. 2013). Rather, seals foraging here could be following predictions from the marginal value theorem (Charnov 1976) where animals foraging in patches of better-than-average quality spend relatively less time there (Thums et al. 2013, see also Jouma'a et al. 2016), which holds provided there is a low cost of travel between dense high-quality patches. Seals foraging downstream of the plateau therefore might have

encountered high densities of prey around eddies and terminated dives because of satiation, depletion of small ephemeral prey patches and/or dispersal of prey, rather than poor patch quality.

The association of seals with eddies (i.e. cores of cyclonic and edges of anticyclonic eddies, respectively) is generally tied to the mechanisms through which nutrients, primary production and consequently prey aggregations are promoted in near-surface waters (Bakun 2006, Della Penna et al. 2015, Le Bras et al. 2016). In this study, deepened prey patches could be driven by anticyclonic eddy activity spawned by the destabilised flow of the ACC downstream of the Kerguelen plateau (Bestley et al. 2018). These structures are responsible for downward export (downwelling) by funnelling particles towards the eddy centre in what is termed the 'wineglass effect' (Waite et al. 2016). Aggregations of primary and secondary production at depth, created by this mechanism, could in turn provide concentrating points for micronekton communities and hence represent potentially profitable foraging patches for seals. Furthermore, because these aggregations are physically mediated by long-lasting downwelling eddies they may be quite predictable over long time-scales for foraging predators. Seals diving to greater depths may also capture larger prey items (Guinet et al. 2014), so that the increased energy expenditure in transiting to greater depths could be offset by improved chances of success and greater returns per capture. However, there was an apparent overprediction in the numbers of seals foraging immediately east of the southern Kerguelen plateau. The oceanography within this region is complex, and characterised by a narrow deep western boundary current carrying cold subpolar waters northward (McCartney and Donohue 2007, Aoki et al. 2008, Bestley et al. 2018). This feature may not be well-captured in the SEAPODYM output, but might influence the prey type, aggregation and advection through the area.

Similar to other populations (McIntyre et al. 2011), female seals foraged almost exclusively south of the SAF whereas the highest SEAPODYM mean prey biomasses were associated with waters north of this front, separated from the south by a steep temperature gradient. Although there may be higher energetic costs for seals associated with thermoregulation in warmer water, small populations of this species do breed on temperate islands (Bester 1980) and the Patagonian coast (Campagna et al. 1995), suggesting that if such costs exist, they are able to cope with them sufficiently to maintain viable populations. Another hypothesis would be that warmer waters increase metabolic rate of poikilothermic prey, thereby improving swimming efficiency and capacity for predator avoidance. However, studies focused on temperature-linked swimming performance in fish have shown that burst speeds are independent of temperature up to about 15°C (Wilson et al. 2001). This suggests that temperature alone is unlikely to be driving this pattern.

The zone from the STF to SAF also represents an important spatial transition from subtropical species assemblages towards Antarctic assemblages (Koubbi et al. 2016). This is mirrored by a southward reduction in the dominance of those SEAPODYM functional groups associated with surface waters (Supplementary material Appendix 1 S2 Fig. A3). A global analysis of deep scattering layer features also showed the SAF to represent a significant biogeographic boundary (Proud et al. 2017). The predominance of elephant seals in waters south of the SAF may therefore reflect significant differences in the mid-trophic species composition, with seals having a selection preference for true Southern Ocean prey assemblages. Indeed, the very low hunting times evident for the north of the region could be a result of seals tending to abort dives early under unfavourable foraging conditions. However, inferences of behaviour north of the SAF should be tempered by the fact that these patterns are generalisations based on few observations (Fig. 5). In contrast to these broadscale patterns, one region of relatively high predicted seal numbers did extend north of the SAF in the eddy-field northwest of the northern Kerguelen plateau. While this high usage was not observed in our post-moult seal distributions, previous studies considering the post-breeding migration (Dragon et al. 2012, Cotté et al. 2015) have shown that southern elephant seals do make use of these waters – along with other Southern Ocean predators – during the austral summer (Delord et al. 2014, Reisinger et al. 2018).

Another spatial mismatch between observed and predicted seal densities occurred south of the sBDY between 70 and 80°E. This was caused by the negative relationship between seal numbers and mean prey biomass. The region falls within the northern limits of the Prydz Bay gyre and the physical environment is strongly influenced by the marginal ice zone (MIZ) with low mesoscale eddy activity (Williams et al. 2010, Bestley et al. 2018). Retention within this gyre could maintain high mean prey biomass with low spatiotemporal variability, as occurs within SEAPODYM. It is relevant to note that the seal dataset used in this study is spatially limited to match the available prey fields. Southern elephant seals do disperse well beyond these bounds (0–140°E, 40–70°S) and show individual specialisation for different regional environments (Bailleul et al. 2010a, Hindell et al. 2017), although not necessarily for three-dimensional habitats (McIntyre et al. 2017). High observed seal density within this area likely represents a northern 'edge' of those seals adopting a MIZ foraging strategy farther south (Labrousse et al. 2015). Therefore, the predator–prey interactions here are likely not shaped by mesoscale eddies, but rather by sea-ice dynamics.

Finally, our GA(M)Ms also predicted few seals foraging over the southern Kerguelen plateau, where dives were shallow but comparatively short (i.e. short hunting times and low dive residuals). Considering the discussion above, low seal densities might suggest poor foraging habitat for pelagically foraging females. While benthic foraging (particularly by males) is common over the shallower northern Kerguelen plateau, the southern plateau is predominantly deeper than 1500 m and hence is less likely to represent key benthic habitat. Importantly however, the region is associated with shoaling upper circumpolar deep water (Roquet et al. 2009),

which is known to be important for pelagically foraging seals (Biuw et al. 2007, Hindell et al. 2016, McMahon et al. 2019). Future work could consider prey abundance, as discussed here, in tandem with the oceanographic processes which explicitly shape vertical availability to predators. The GA(M)Ms performance could be improved by considering these for inclusion alongside metrics of prey distribution. Our focus was on representing dynamic prey distributions, but prey and predators are obviously influenced by a myriad of biophysical processes.

Conclusions

We show how a model representation of micronekton prey fields, difficult to observe directly, give new insights into the ecological processes influencing behaviour of Southern Ocean predators. This study focused on southern elephant seals but paves the way for studies that extend beyond deep divers, consider different foraging strategies and evaluate multi-species predator assemblages. Improved ability to disentangle mechanisms governing the distributions of prey and their dependant predators will be of increasing importance in predicting species' responses to rapid Southern Ocean change.

Data availability statement

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.vhhmgqnqn> (Green et al. 2020).

Acknowledgements – The Kerguelen Islands ARGOS seal tracking and dive data were collected as part of a collaboration between IMOS and SNO-MEMO (PI C. GUINET). Data were sourced from the Integrated Marine Observing System (IMOS). IMOS is a national collaborative research infrastructure, supported by the Australian Government. It is operated by a consortium of institutions as an unincorporated joint venture, with the Univ. of Tasmania as lead agent. We are grateful to Olivier Titaud for technical support with SEAPODYM. This work was strengthened by thoughtful feedback from three anonymous reviewers.

Funding – Field work at Kerguelen was conducted as part of the IPEV programs no. 109 (PI H. WEIMERSKIRCH) and no. 1201 (PI C. GILBERT) in collaboration with IMOS. This study received support from the European H2020 International Cooperation project MESOPP (Mesopelagic Southern Ocean Prey and Predators, <www.mesopp.eu/>). DBG was funded through a Tasmania Graduate Research Scholarship. SB is supported by the Australian Research Council under DECRA award DE180100828. Additional funding support was received through Institut Polaire Paul Emile Victor. Grant Number: 1201.

Author contributions – All authors contributed to the design and development of the work. DBG, with contributions from MAH, performed the analyses. DBG wrote the manuscript with substantial contributions from SB, RT, SPC, PL, CRM, CG and MAH. All authors read and approved the manuscript prior to submission.

Permits – All tagging procedures were approved and executed under the Univ. of Tasmania Animal Ethics Committee guidelines; project: A0017025, Monitoring Antarctic Predators in the Southern Ocean.

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Supplementary material (available online as Appendix ecog-04939 at <www.ecography.org/appendix/ecog-04939>). Appendix 1.